

A NEW SPECIES OF *SEPIA*
(CEPHALOPODA, SEPIIDAE) FROM SOUTH AFRICA

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(With 14 figures and 4 tables)

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ABSTRACT

A new species of the genus *Sepia* is described from the Atlantic Coast of the Cape Peninsula, South Africa. *Sepia pulchra* sp. nov. is the fifth species of *Sepia* maturing at a small size (MLd approx. 20 mm) to be recorded from South African waters. The female animal most closely resembles *S. dubia*, which has been placed in the problematic subgenus *Hemisepius*. However, the shell of *S. pulchra* indicates that this species is more closely related to members of the subgenus *Sepia* s.s. The use of the ventral keels on the mantle, and the position of spermatophores on the hectocotylus, are illustrated for the first time in sepiids.

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INTRODUCTION

On a series of SCUBA dives off the Atlantic Coast of the Cape Peninsula a number of small sepiids were collected by one of us (W.R.L.). These specimens were originally thought to be *Sepia dubia*, a species known from a single female specimen (Adam & Rees 1966: 119–120), also from South Africa.

On closer examination the newly acquired specimens were found to differ from the description of *S. dubia* in the sucker arrangement on the ventral arms and the structure of the shell. A re-examination of the holotype of *S. dubia*

showed that the female animals of both *S. dubia* and the new specimens do not seem to differ significantly (the male of *S. dubia* being unknown). The shells, however, are quite different.

The measurements, indices and abbreviations used in this paper are defined by Roeleveld (1972: 196). Additional measurements and counts are as follows:

- EMLv — effective ventral mantle length, i.e. excluding that part of the mantle lying outside the limits of the ventral keels; measured along the ventral midline from the anterior edge of the mantle to the posterior limit of the keels.
- HcL — length of the hectocotylized (left ventral) arm.
- MHL — length of the (proximal) modified portion of the hectocotylus, from the most proximal suckers to the first normal (distal) suckers; the length of the modified portion is calculated as a percentage of the total length of the hectocotylized arm (HcL) and not of the mantle length.

Club suckers — the total number of suckers on the tentacular club.

Furthermore, an estimate of the maturity stage of each specimen is indicated by a roman numeral I–III (see Table 1). Since the sex, size and maturity

TABLE 1
Definition of maturity stages.

<i>Maturity stage</i>	<i>Male</i>	<i>Female</i>
I: immature	Spermatophores absent; testis small, undeveloped.	Ovary and nidamental glands small, undeveloped.
II: maturing	Testis and accessory reproductive glands partially developed, but spermatophores absent.	Ovary and nidamental glands partially developed; no eggs visible in ovary.
III: mature	Spermatophores present in Needham's sac, penis and/or on hectocotylus.	Nidamental glands large; fully developed eggs present in ovary.

stage affect the morphology (especially the degree of modification of the hectocotylus in males), these conditions are relevant in comparing specimens. A particular specimen can then conveniently be designated, for example, ♂ III 24, indicating a mature male with a dorsal mantle length of 24 mm.

Sepia pulchra sp. nov.

Figs 1–14; Tables 2–4

Material

Holotype: SAM–S1036, ♂ III 17, Llandudno, Cape Peninsula, 25 m, collected by W. R. Liltved, 11 October 1982, SCUBA; deposited in the South African Museum.



Fig. 1. *Sepia pulchra* sp. nov. Dorsal view of holotype, SAM-S1036, ♂ III 17. Scale = 5 mm.

Paratypes: SAM-S822, ♂ III 22, Hottentots Huisie, Cape Peninsula, 15 m. SAM-S982, ♀ III 21, Bakoven, Cape Peninsula, 21 m. SAM-S1007, ♂ III 16, ♀ II 17, Llandudno, Cape Peninsula, 25 m (same data as holotype). SAM-S1029, ♂ III 19, ♀ II 21, Llandudno, Cape Peninsula, 26 m. SAM-S1030, ♀ III 22, Llandudno, Cape Peninsula, 40 m. SAM-S1031, ♂ III 17, ♂ III 18, Llandudno, Cape Peninsula, 30 m. SAM-S1032, ♂ III 19, ♀ III 22, Llandudno, Cape Peninsula, 30 m. SAM-S1033, ♂ III 20, ♀ III 24, Llandudno, Cape Peninsula, approx. 50 m. SAM-S1034, ♂ III 15, Hottentots Huisie, Cape Peninsula, 15 m. SAM-S1038, ♀ III approx. 19, Llandudno, Cape Peninsula, 32 m. SAM-S1039, ♀ III 19, Llandudno, Cape Peninsula, 35 m.

Diagnosis

Mantle with numerous complex dorsal papillae and fleshy ventral keels; suckers biserial on arms I-III and distally on arms IV, quadriserial proximally on arms IV; sexual dimorphism involving sucker enlargement on arms II and sometimes III and modification of sucker shape and size on right arm IV in males; tentacular club with subequal suckers; shell not calcified, delicate, broadly oval, with phragmocone extending to anterior margin, with reflexed inner cone and no posterior spine.

TABLE 2
Sepia pulchra sp. nov. Indices and counts for males.

	SAM-S822 ♂ III 22	SAM-S1033 ♂ III 20	SAM-S1029 ♂ III 19	SAM-S1032 ♂ III 19	SAM-S1031 ♂ III 18	Holotype SAM-S1036 ♂ III 17		SAM-S1031 ♂ III 17	SAM-S1007 ♂ III 16	SAM-S1034 ♂ III 15	<i>n</i>	Mean	Range MLd 15-22 mm
MLv	90.9	95.0	105.3	89.5	94.4	100.0	100.0	94.1	93.8	100.0	9	95.9	89.5-105.3
EMLv	72.7	80.0	94.7	73.7	77.8	82.4	82.4	82.4	81.3	86.7	9	81.3	72.7-94.7
MW	77.3	60.0	73.7	73.7	72.2	76.5	76.5	82.4	81.3	73.3	9	74.5	60.0-82.4
HL	40.9	55.0	63.2	63.2	55.6	58.8	58.8	58.8	62.5	60.0	9	57.6	40.9-63.2
HW	59.1	55.0	68.4	63.2	61.1	64.7	64.7	58.8	62.5	66.7	9	62.2	55.0-68.4
FL	100.0	95.0	89.5	94.7	100.0	100.0	100.0	105.9	100.0	93.3	9	97.6	89.5-105.9
FW	22.7	20.0	26.3	21.1	22.2	23.5	23.5	29.4	25.0	26.7	9	24.1	20.0-29.4
AL I	40.9	45.0	47.4	52.6	44.4	52.9	52.9	52.9	43.8	46.7	9	47.4	40.9-52.9
II	45.5	50.0	47.4	47.4	50.0	58.8	58.8	58.8	56.3	53.3	9	51.9	45.5-58.8
III	50.0	50.0	57.9	57.9	55.6	58.8	58.8	58.8	56.3	53.3	9	55.4	50.0-58.8
IV R	59.1	55.0	57.9	57.9	66.7	70.6	70.6	64.7	62.5	60.0	9	61.6	55.0-70.6
HcL	54.5	50.0	52.6	57.9	61.1	58.8	58.8	58.8	62.5	60.0	9	57.4	50.0-62.5
MHL						•							
(% HcL)	58.3	60.0	60.0	45.5	54.5	70.0	70.0	60.0	60.0	55.6	9	58.2	45.5-70.0
TL R	81.8	125.0	142.1	89.5	55.6	105.9	105.9	100.0	125.0	120.0			
L	77.3	135.0	105.3	94.7	88.9	100.0	100.0	82.4	150.0	173.3			
Tel	13.6	15.0	26.3	21.1	16.7	—	—	17.6	25.0	20.0	8	19.4	13.6-26.3
Club	60	57	57	60	59	59	59	60	68	—	8	57-68	

Description

The animals are small, attaining maturity at a dorsal mantle length of 15–22 mm in males and 19–24 mm in females.

The mantle is broadly oval, its anterior margin convex dorsally and deeply emarginate ventrally around the funnel. The fins are of variable width, usually fairly wide, beginning relatively far back (the distance between the anterior ends of the mantle and fin is 23–33% MLD). Posteriorly the fins are rounded and separate.

The colour is reddish-brown dorsally on the mantle, head and arms, with the pigmentation of the mantle extending on to the bases of the fins. Mid-dorsally on the mantle there is a large oval purplish patch. The entire dorsal surface of the mantle, head and arms is covered with tubercles of variable size and complexity. The tubercles occur as three main types: simple tubercles, complex turrets, and even more complex flat oval tubercles. The larger tubercles are arranged in a distinct pattern that can be traced in all the specimens, although not all the tubercles of the pattern are readily distinguishable in every specimen. The degree of distinction of these large tubercles depends on the preservation and degree of skin contraction or 'wartiness' of the specimen; in addition, a particular large tubercle may have an overall flat oval appearance in one specimen and be more turret-like in another.



Fig. 2. *Sepia pulchra* sp. nov. Ventral view of holotype, SAM-S1036, ♂ III 17.
Scale = 5 mm.

TABLE 3
Sepia pulchra sp. nov. Indices and counts for females.

	SAM-S1033 ♀ III 24	SAM-S1032 ♀ III 22	SAM-S1030 ♀ III 22	SAM-S1029 ♀ II 21	SAM-S982 ♀ III 21	SAM-S1039 ♀ III 19	SAM-S1007 ♀ II 17	n	Mean	Range MLD 17-24 mm
MLV	100,0	100,0	100,0	104,8	100,0	100,0	94,1	7	99,8	94,1-104,8
EMLV	79,2	86,4	90,9	90,5	71,4	89,5	88,2	7	85,2	71,4-90,9
MW	70,8	72,7	72,7	76,2	76,2	84,2	88,2	7	77,3	70,8-88,2
HL	58,3	63,6	68,2	57,1	52,4	57,9	76,5	7	62,0	52,4-76,5
HW	50,0	59,1	59,1	66,7	57,1	57,9	64,7	7	59,2	50,0-66,7
FL	87,5	100,0	90,9	95,2	104,8	105,3	105,9	7	98,5	87,5-105,9
FW	25,0	18,2	22,7	23,8	28,6	26,3	23,5	7	24,0	18,2-28,6
AL I	37,5	40,9	36,4	42,9	38,1	42,1	47,1	7	40,7	36,4-47,1
II	41,7	40,9	40,9	42,9	42,9	47,4	52,9	7	44,2	40,9-52,9
III	45,8	45,5	40,9	52,4	47,6	52,6	58,8	7	49,1	40,9-58,8
IV	50,0	54,5	50,0	52,4	52,4	57,9	58,8	7	53,7	50,0-58,8
TL R	162,5	118,2	145,5	157,1	128,6	115,8	141,2			
L	166,7	127,3	136,4	171,4	157,1	100,0	200,0			
Tcl	20,8	22,7	18,2	23,8	23,8	21,1	23,5	7	22,0	18,2-23,8
Club suckers	63	66	56	—	61	61	62	6		56-66

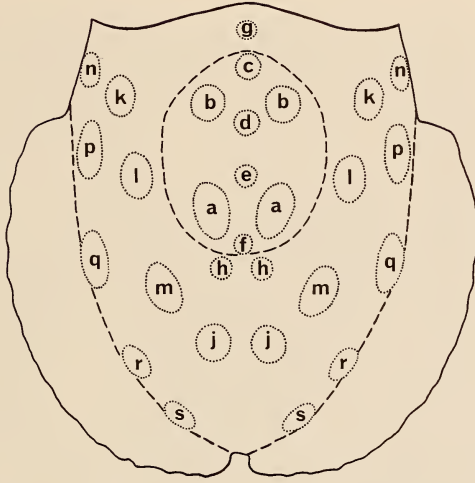


Fig. 3. *Sepia pulchra* sp. nov. Diagrammatic representation of relative sizes and distribution of the larger tubercles on the dorsal mantle surface.

In most specimens (including the holotype) three larger tubercles form cirri over each eye. On the mantle the pattern is most readily traced from the dorsal median patch. The patch bears two large, flat, oval tubercles (Fig. 3, a) posteriorly and two turrets (Fig. 3, b) anteriorly; four slightly smaller turrets (Fig. 3, c-f) run along the midline of the patch. The first of these median turrets (Fig. 3, c) is sometimes enlarged, forming a group of three with the two lateral turrets (Fig. 3, b). The median line of turrets on the patch is continued anteriorly by a single turret (Fig. 3, g) between the patch and the anterior mantle margin. Immediately posterior to the patch a pair of turrets (Fig. 3, h) straddles the dorsal midline; a second and somewhat larger pair of turrets (Fig. 3, j) occurs halfway between the posterior end of the patch and the posterior mantle margin. The latter pair of turrets (Fig. 3, j) is part of a series of eight tubercles (Fig. 3, j-m) that are arranged around the patch in a line roughly parallel to the lateral and posterior margins of the mantle. The six anterior tubercles of this lateral line are usually flat oval tubercles, whereas the posteriormost pair (Fig. 3, j) is turret-like. A marginal line of tubercles (Fig. 3, n-s) lies outside the lateral line. The first two tubercles (Fig. 3, n) of the marginal line lie anterior to the fins and the remaining tubercles are on the fin bases, alternating in position with the tubercles of the lateral line. The marginal line usually consists of ten flat oval tubercles. The spaces between the primary tubercles are filled with smaller tubercles ranging from simple to fairly complex, with several protrusions. All the principal tubercles described above are present in the holotype, but the posteriormost four tubercles (Fig. 3, r-s) of the marginal line are not very clearly distinguishable.

The ventral surface of the mantle, head and arms IV is buff in colour and forms a sole, made up of a pair of fleshy keels on the mantle and the swollen under-surfaces of the ventral arms (Fig. 2). The keels do not extend to the posterior end of the mantle, nor to the fin bases laterally; the lateral and posterior areas between the keels and fin bases are a somewhat lighter shade of the colour of the dorsal mantle surface.

The arms are short and stout, with well-developed fleshy protective membranes. The upper three pairs of arms are joined by an interbrachial membrane. Arms I and II are trapezoid in cross-section, with a flattened aboral surface; arms III and particularly arms IV bear lateral keels.

The suckers are globose, with small apertures. The sucker rings have a smooth inner edge, without teeth.

In the females, the suckers are biserial on arms I, II and III, though when the arms are compressed the suckers may give the appearance of being triserially or even quadriserially arranged on the proximal half of the arm, this compression most commonly occurring on the lateral arms (II and III). The suckers are largest near the base of the arm and gradually decrease in size distally. On the ventral arms of the females the suckers are quadriserially arranged on the proximal half to two-thirds of the arm but become biserial on the distal part.

In males the left ventral arm is hectocotylized. The proximal two-thirds of the arm is modified: the oral arm surface is wider than usual and bears numerous transverse folds. The suckers of the modified portion are reduced in size and form two longitudinal series of suckers on either side of the ridged oral region. The dorsal suckers clearly pertain to two longitudinal series as the suckers alternate in a zigzag manner. The two ventral series of suckers have merged to form an almost straight longitudinal row. Distal to the modified portion, the suckers are biserial.

In the holotype, the hectocotylus bears two pairs of widely separated suckers proximally. The dorsal and ventral margins of the modified region each bear eleven alternating lateral and medial suckers. Distally the arm bears seven to eight pairs of biserial suckers; the first few pairs of biserial suckers are larger than those in the modified region, but the sucker size decreases towards the arm tip. In the other males the number of suckers bordering the modified portion of the hectocotylus varies from ten to fourteen on either side of the ridged region.

The right ventral arm is also modified in males. Proximally there is a group (usually eight) of large globose suckers, irregularly arranged. Following these there are two to four medium suckers and two to four minute suckers; these occur either as a transverse row of four medium-sized suckers followed by two minute suckers, one on each extreme edge of the oral surface, as in the holotype, or as one medium-sized sucker on each extreme edge of the oral arm surface followed by minute suckers in a transverse row of four. This proximal group of suckers, which occupies about 40 per cent of the arm length, is followed by a pair of highly modified suckers (usually the 15th and 16th from the arm base). These suckers (Fig. 5) are greatly enlarged and asymmetrically



Fig. 4. *Sepia pulchra* sp. nov. Hectocotylus and right ventral arm of holotype, SAM-S1036, ♂ III 17. Scale = 2 mm.



Fig. 5. *Sepia pulchra* sp. nov. Detail of modified suckers on right ventral arm of holotype, SAM-S1036, ♂ III 17. Scale = 1 mm.

elongate, with the ring proximal to the main body of the sucker, their overall shape being reminiscent of the pitcher plant (*Nepenthes*). The modified suckers are followed by a pair of very small suckers. In contrast, the next pair (usually the 19th to 20th suckers) is much larger, attaining at least the size of the medium suckers of the proximal group. Thereafter 24 to 28 suckers gradually reduce in size to the arm tip and are generally biserially arranged, though contraction of the arm may sometimes give a quadriserial appearance to the suckers on the middle of the arm. In one specimen (SAM-S1007, ♂ III 16) a second pair of suckers (the 19th to 20th) is modified as well as the 15th to 16th suckers on the right ventral arm, though not to the extent of the more proximal pair.

A further form of sexual dimorphism is shown in the enlargement of several suckers towards the tips of the lateral arms in males. The most marked sucker enlargement occurs on arms II, where there are usually three (but occasionally four) pairs of enlarged suckers in the 8th to 12th pairs from the arm base. A tendency towards enlargement of suckers is sometimes also shown on arms III. Where present, this enlargement affects one to three (usually two) pairs of suckers in the 10th to 14th rows from the arm base. In the holotype there are seven enlarged suckers on each arm II; these suckers pertain to the 8th to 11th pairs on left II and the 9th to 12th pairs on right II. There is no marked enlargement of suckers on arms III in the holotype.

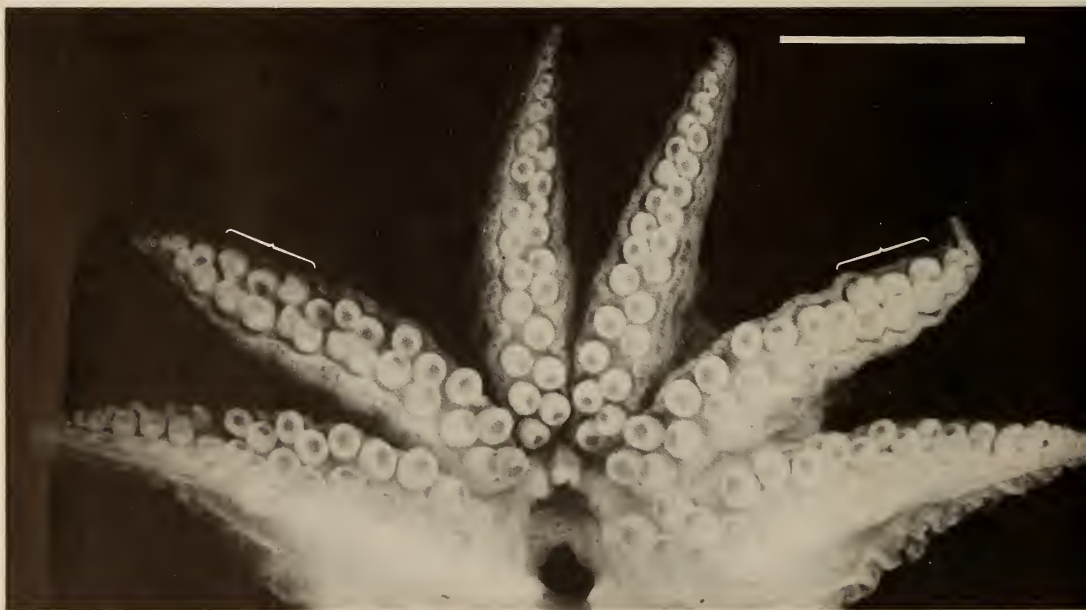


Fig. 6. *Sepia pulchra* sp. nov. Dorsal and lateral arms of holotype, SAM-S1036, ♂ III 17, showing enlargement of distal suckers on arms II (brackets). Scale = 5 mm.

The tentacular club is short and broad, somewhat recurved, and bears subequal suckers in transverse rows of four to six. The dorsal protective membrane is well developed and separate proximally from the ventral protective membrane, which curves around the base of the club. The natatory membrane is broad and continues along the tentacular stalk beyond the proximal end of the club. A terminal pad found on the club of many *Sepia* species, e.g. *Sepia faurei* (Roeleveld 1972, fig. 16b) and *S. robsoni* (Adam & Rees 1966, pl. 46, fig. 279), is situated at the anterior end of the dorsal protective membrane and is of similar size and shape to the club suckers. The dorsal surface of the club bears several transverse rows and a number of scattered chromatophores.

The beaks, radula and spermatophore are illustrated in Figures 8 and 9. The lower beak of SAM-S1033, ♀ III 24, has the following dimensions (after Clarke 1962 and Wolff 1982): rostral length (RL) 0,86 mm, wing length (WL) 3,24 mm, rostral tip to inner margin of wing (RW) 4,08 mm, crest length (CL) 3,26 mm, hood length 1,50 mm, jaw-angle width (JW) 1,66 mm. The hood and lateral wall are darkened around the rostrum and jaw angle, but leave a clear strip between them along the jaw edge. The darkening of the lateral wall gradually diminishes posteriorly and the wing is only slightly pigmented. The jaw angle is indistinct and obtuse, and is not obscured by a wing fold. The lateral wall has no distinct ridge or fold and there is no indentation in its posterior margin. The wing is long in relation to the rostrum (WL/RL 3,8).

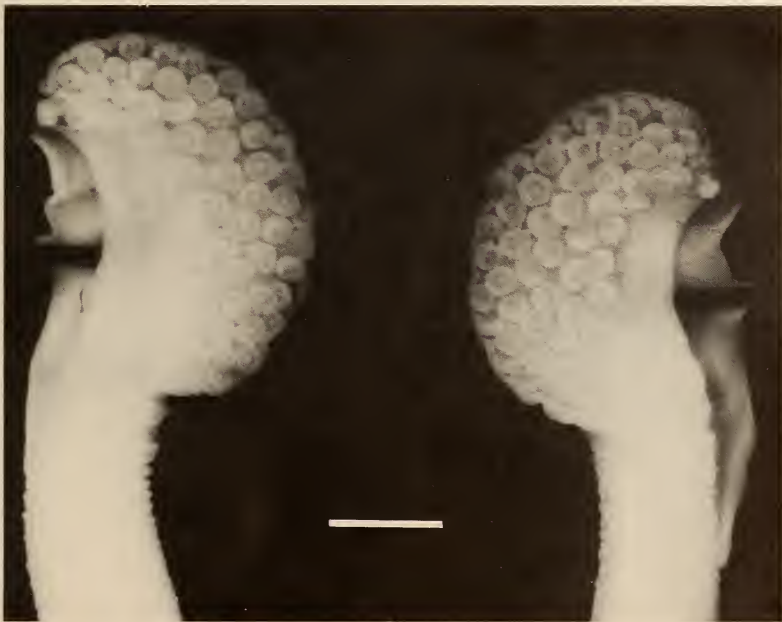


Fig. 7. *Sepia pulchra* sp. nov. Tentacular clubs, SAM-S822, ♂ III 22.
Scale = 1 mm.

TABLE 4
Sepia pulchra sp. nov. Indices for shells.

	SAM-S822 ♂ III 22	SAM-S982 ♀ III 21	SAM-S1038 ♀ III c. 19	SAM-S1039 ♀ III 19	Holotype	n	Mean	Range
					SAM-S1036 ♂ III 17			
L in mm	21	19	19	c. 19	16	5		16-21
W	52,4	63,2	63,2	c. 57,9	56,3	5	c. 58,6	52,4-63,2
Str z	c. 71,4	c. 57,9	63,2	c. 52,6	62,5	5	c. 61,5	c. 52,6-c. 71,4

The shell is not calcified and is broadly oval, becoming somewhat angular anteriorly; posteriorly the shell is broad, with a strong ventral curvature and a dorsal hump over the posterior end of the phragmocone. There is no posterior spine. The dorsal surface of the shell is finely reticulate and shows no distinct median ridge; the striae of the phragmocone are clearly visible through the thin dorsal shield. The phragmocone covers virtually the entire length of the shell and is very thin; the ventral surface is flat or somewhat concave, with at most an indistinct median groove; the striated zone is long and triangular, the striae wavy with an overall convex shape. The inner cone is reflexed and fused to the outer cone; in the holotype it is narrow, the limbs of the inner cone extending anteriorly along the lateral edges of the striated zone; in a larger shell (SAM-S1038, Fig. 9A) the inner cone is rather broader laterally, then tapers rapidly and twists, curving over the lateral edge of the striated zone. The outer cone is very broad laterally but narrow posteriorly, separating the posterior end of the inner cone from the shell edge by a narrow strip of outer cone.

Remarks

The female animals of *Sepia pulchra* are difficult to distinguish from *S. dubia*. Adam & Rees (1966: 120) described the arm suckers of *S. dubia* as being biserial, but re-examination of the holotype, ♀ II 17, showed that, as in

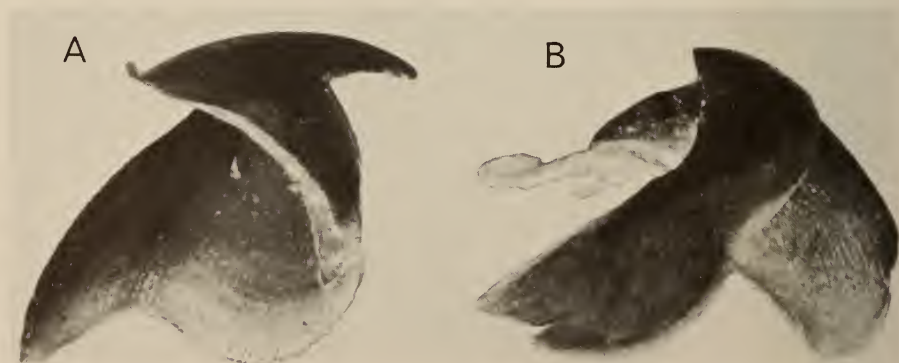


Fig. 8. *Sepia pulchra* sp. nov. Beaks, SAM-S1033, ♀ III 24. A. Upper beak, rostral length 1,0 mm. B. Lower beak, rostral length 0,86 mm.

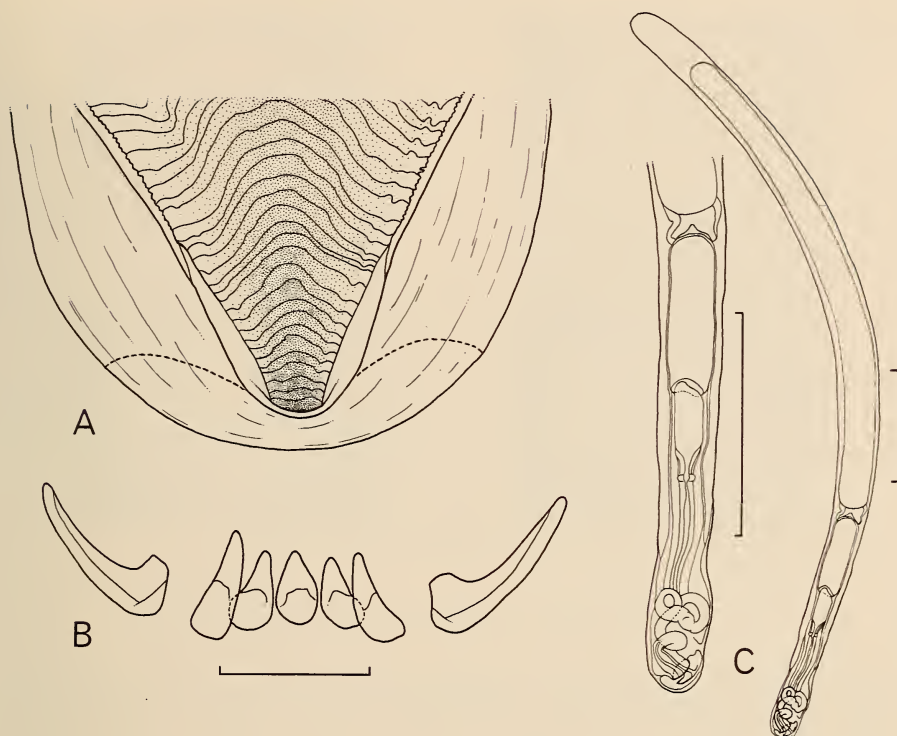


Fig. 9. *Sepia pulchra* sp. nov. A-B. SAM-S1038, ♀ III approx. 19. A. Detail of posterior part of shell, ventral view. B. One row of teeth from radula. C. SAM-S822, ♂ III 22. Spermatophore from Needham's sac, with enlargement of the oral end. Each scale = 0,5 mm.

S. pulchra, the suckers are biserial on arms I-III, with a tendency to irregularity on the lateral arms due to crowding, and quadriserial in the middle of arms IV.

According to Adam & Rees (1966: 119), in the holotype of *S. dubia* 'the dorsal surface of mantle, head and arms is covered with well spaced, round papillae, creating a very rugose appearance. . . . On the dorsal surface of the mantle, approximately in the middle, there are two oval patches of contracted papillae, one on each side of the median line, and a third one anteriorly near the mantle-margin.'

On careful scrutiny, the arrangement of the tubercles of the holotype of *S. dubia* was found to be remarkably like that of *S. pulchra*. The oval patch on either side of the midline in *S. dubia* corresponds with the two main complex tubercles (Fig. 3, a) in *S. pulchra*; the third anterior patch of *S. dubia* is much larger than the corresponding tubercle, c, in *S. pulchra* and may represent an amalgamation of tubercles c and d of *S. pulchra*, as in *S. dubia* there is only this one large tubercle between the two smaller tubercles, g and e, found in both

species. The area of the median tubercles (a-f) does not appear as a distinct dorsal patch in *S. dubia*.

The remaining tubercles (h-s) on the dorsal mantle surface of *S. dubia*, though not very distinct, appear to show the same arrangement as in *S. pulchra*, with the exception of tubercle n. In *S. dubia* tubercle n lies immediately above, rather than in front of, the anterior fin margin, since the distance between the anterior margins of the mantle and the fin is less (12,5% MLd) in *S. dubia* than in *S. pulchra* (23-33% MLd).

At this stage it is not possible to assess the significance of the differences in the tubercles (c, d, n) and the presence or absence of the median patch in separating the two species, since *S. dubia* is known from a single female specimen. However, the two species differ markedly in their shells. *Sepia dubia* has a *Hemisepius*-like shell, with the phragmocone having an inverted triangular shape and occupying little more than half the shell length, as in *Sepia (Hemisepius) typica*. The shell of *S. pulchra*, on the other hand, has an overall resemblance to that of *S. tuberculata*, though being much more fragile; this further weakens the distinction between the subgenera *Sepia* and *Hemisepius*.

AFFINITIES WITH RELATED SPECIES

Sepia pulchra is the fifth small species of *Sepia* to be found in South African waters and further compounds, rather than resolves, the intriguing problem of their interrelationships. The other species are *Sepia robsoni*, *S. faurei*, *Sepia (Hemisepius) typica* and *S. (Hemisepius) dubia*. All five species are small, maturing at a dorsal mantle length of about 20 mm. They all have a very broad mantle (MW 60-90% MLd), the anterior margin of which is convex dorsally and deeply emarginate ventrally, and fleshy keels ventrally on the mantle; suckers that are biserial, at least on arms I, II and III; and a tentacular club bearing small sub-equal suckers and protective membranes that are separate proximally.

Sepia typica, *S. dubia* and *S. faurei* have a *Hemisepius*-like shell with an abbreviated phragmocone, whereas that of *S. pulchra* is typically sepiid. The shell of *S. robsoni* is virtually unknown. Massy (1927: 160) mentioned only that 'The calcareous portion of the shell has unfortunately been totally dissolved, only the membranous part remaining'. Adam & Rees (1966: 121) found the shell to be in poor condition and compared it to *S. hieronis* and *S. insignis*. If the phragmocone of *S. robsoni* was not of the normal sepiid type, Adam & Rees would certainly have mentioned it.

The convenient separation of these five species into three with a hemisepiid shell and two with a normal shell is not borne out by other characters of the animals. *Sepia robsoni* and *S. faurei* both have dorsal arms with finger-like tips, devoid of suckers, whereas *S. dubia* and *S. pulchra* are virtually indistinguishable at present except by the shell characters.

The resolution of the relationships within this group of five species must await the collection of further specimens of *S. robsoni*, *S. dubia* and *S. faurei*,



Fig. 10. *Sepia pulchra* sp. nov.
Dorsal view of shell of holotype,
SAM-S1036, ♂ III 17.
Scale = 5 mm.



Fig. 11. *Sepia pulchra* sp. nov.
Ventral view of shell of holotype,
SAM-S1036, ♂ III 17.
Scale = 5 mm.

each of which is known only by the holotype. The problem is further complicated by the small size of the animals and the difficulty in extracting the very delicate shells.

BIOLOGICAL OBSERVATIONS

The collection of live specimens of *Sepia pulchra* has provided the opportunity to add a few notes on the biology of the species. The sole, formed by the fleshy keels on the mantle (Fig. 12) and the swollen under-surfaces of the ventral arms, is found in several species (see above), but its use has not been figured before. Since most of the specimens of *S. pulchra* were observed (by W.R.L.) adhering to vertical rock faces in the head-down position, the sole must be of considerable importance in maintaining this position. Camouflage against the background would then be effected by the extensive tuberculation of the dorsal surface of the mantle, head and arms; the well-known ability of sepiids to undergo extreme variation in colour pattern would be a further contributing factor. The reason for the pigmentation of the part of the ventral mantle surface between the keels and fin bases in this species became obvious on observing animals in an aquarium. When an animal adheres to the hard substrate, these parts of the mantle are clearly visible (Fig. 12) and thus also require to be camouflaged, whereas in species that settle on a sandy substrate this part of the mantle is not usually visible.

Two mature males (SAM-S1031) were found to have spermatophores attached to the hectocotylus, allowing the position of the spermatophores to be



Fig. 12. *Sepia pulchra* sp. nov., adhering to rock by fleshy keels of mantle; in this instance the ventral arms are not participating in the adhesion; SAM-S1039, ♀ III 19, photographed in aquarium.

illustrated for the first time (as far as could be established). While copulation has been observed in *S. officinalis* (Grimpe 1926; Bott 1938; Tinbergen 1939), it has been found difficult to see the actual transfer of spermatophores, since this is obscured by the intermingled arms of the mating animals. Bott (1938: 155) has given a detailed description of spermatophore transfer from male to female: the modified (proximal) portion of the hectocotylus, which bears a number of transverse folds on the oral surface bordered by a reduced number of rudimentary suckers, forms a groove connecting the funnel of the male with the bursa copulatrix on the buccal membrane of the female. According to Bott's observations the hectocotylus thus functions as a passage for the spermatophores.

The structure of the hectocotylus of *S. pulchra* is basically like that of *S. officinalis*. However, observations on *S. pulchra* suggest that the spermatophores not only pass along the hectocotylus but are actually attached to the arm (Figs 13–14). Furthermore, Figure 14 shows that the spermatophores are attached to the hectocotylus not only in the ridged area between the rudimentary suckers, but also on the lateral part of the arm outside the sucker rows. Though the attachment of spermatophores to the hectocotylus is not very firm, since the spermatophores are fairly easily dislodged in preserved specimens, the strength of attachment was nevertheless sufficient to maintain the spermatophore position during capture, transport and preservation of these two specimens. The means of attachment of the spermatophores to the hectocotylus would appear to be mucous, since there was no evidence of any structural attachment, nor did the suckers appear to play a part.

Examination of the bundle of spermatophores of *S. pulchra* illustrated in Figure 13 showed the spermatophores to have discharged and be interspersed



Fig. 13. *Sepia pulchra* sp. nov. Position of spermatophore bundle on modified portion of hectocotylyzed left ventral arm; SAM-S1031, ♂ III 17. Scale = 2 mm.



Fig. 14. *Sepia pulchra* sp. nov. Position of individual spermatophores on hectocotylus, after most of spermatophore bundle removed; SAM-S1031, ♂ III 18. Scale = 2 mm.

with sperm reservoirs, the bundle being held together by mucus or perhaps cement from the cement bodies of the spermatophores. The spermatophores in this bundle were all held together by their oral ends, an apparently unnatural condition possibly attributable to the capture and handling of the animal. However, the spermatophores illustrated in Figure 14, which had also ejaculated, were attached to the hectocotylus by their aboral ends, an orientation more consistent with the observation that spermatophores leave the penis aboral-end first and are carried to the female oral-end first, being held in position by the male until the spermatophores have discharged and the sperm reservoirs are fixed by the cement to the female, either in the mantle cavity or on the buccal membrane (Drew 1919: 398, 413).

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